UNILATERALITY IN INFESTATIONS OF THE MOTH EAR MITE

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The gamasine mite *Myrmonyssus phalaenodectes* Treat (1954) is a widely distributed parasite in the tympanic organs of noctuid moths, chiefly those of the genus *Leucania*. Its colonies, whether founded by a single female or by several, occupy and destroy the function of one but not both of the host's ears. Each female can produce from 80 to 100 eggs. The young develop to maturity on the original host and the fertile females then seek another moth on which to repeat the cycle. A large colony fills the three chambers of the ear to overflowing. As the maturing females leave the ear, they populate both sides of the head, neck, and prothorax of the host, whence they leave, a few at a time, to found colonies of their own. Regardless of the age, size, or condition of the colony, one ear is normally left unoccupied and undamaged. Left and right sided infestations are about equally common, and mites reared on one side of the original host may found colonies on the opposite side of its successor.

In the unilaterality of its colonies, the moth ear mite contrasts sharply with most insect-infesting mites, which tend to distribute themselves symmetrically on the host's body, often with astonishing precision (Cooper, 1955). In such relationships the equilibrium of the insect is undisturbed, while the damage to the host, if any, is not more severe for being equally distributed. The moth ear mites, on the other hand, make the moth "deaf in one ear," and were they to invade both sides they would leave their host unable to detect the high pitched sounds of bats and perhaps of other predators (Roeder and Treat, 1957). They might thus expose both their hosts and themselves to early extinction. Though it seems unlikely that the mites apprehend this danger, they nevertheless appear to avoid it quite systematically. How does this come about? Are bilateral colonies sometimes formed, only to be devoured by bats or to render the moths incapable of

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flight and therefore less likely to be taken by the collector? Is it physiologically impossible for the mites to use both ears? Are the moths somehow unsymmetrical in the attractiveness of their two sides, or are the mites congenitally right or left handed?

To most of these questions it is easy to show that the answer is No. That unilaterality is not required for the development of the colony is proved by the experiment of placing one or more gravid females in each of the two tympanic recesses of the same moth. The result is usually a colony on both sides. As long as the moth is sheltered in the laboratory it shows few ill effects (other than deafness) from its parasites, and the two colonies mature normally. A single ovipositing female transferred to the opposite ear will sometimes return to her brood, but she may instead continue egg laying in her new location, thus producing a bilateral colony all by herself. Except for such experiments, bilateral colonies are about as rare in the laboratory as they are in the field, where only two have been discovered among nearly 1,000 infestations.

Were every colony the work of a single female there would be no problem; her attraction to her brood, and later the gregariousness of her offspring would tend to localize the mites in whichever ear she chanced to occupy. But though such simple colonies are common, compound colonies with ovipositing females numbering eight or more are often seen, especially in midsummer when the incidence of infestation is at its peak. If, as is believed, the young females commonly leave their old hosts and find new ones while the insects are feeding on flowers, it must often happen that a single moth will take aboard several wanderers, one or a few at a time, from several sources. Indeed it is only in this way that cross-fertilization could be achieved, since the males do not wander, and the only males present in a colony are those that develop there. When several fertile female mites—say 8 or 10—are placed at random on both sides of a previously mite-free moth and the insect is then confined in a jar or cage, a typical unilateral compound colony usually develops. Similar results have been noted when mite-free moths are kept in closed jars with infested moths or with wandering female mites (Figure 1).

As far as one can tell, the mites are blind, deaf, and dumb. In glass containers they do not appear to follow trails, either

their own or others'. On a living moth held by upraised wings under an entomological microscope, they show no tendency to congregate, but push about slowly and singly, as though at random, among the hairs of the head and thorax. From two to several

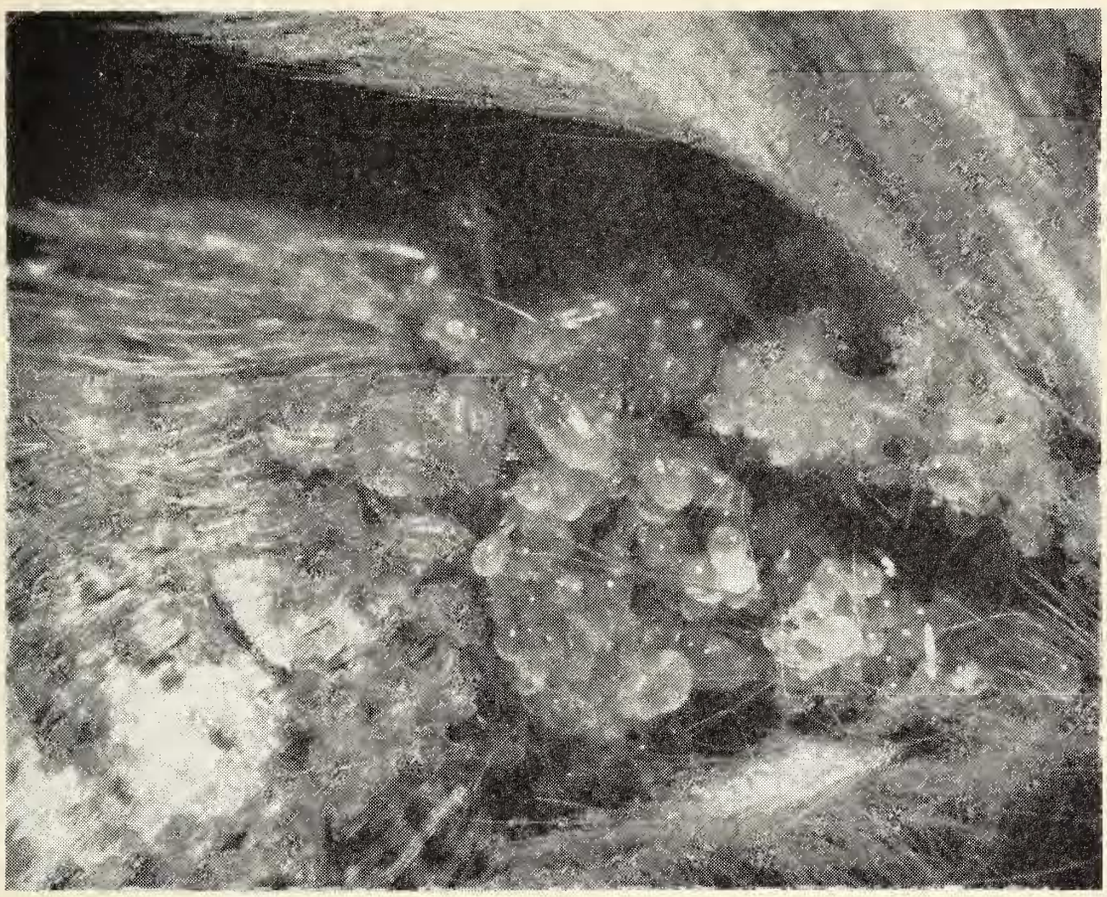

Figure 1. A living colony of moth ear mites in the right tympanic area of an armyworm moth, *Pseudaletia unipuncta*, ♀. The moth was taken, mite-free, on 21 September, 1957, and was confined in a glass jar for five days with an infested *Leucania phragmatidicola* ♂, taken at the same time in Tyringham, Massachusetts. Photographed 30 September, 1957, by Dr. A. B. Klots. Ten gravid female mites are visible, together with several larvae, three deutonymphs, and many eggs. Many more mites and eggs occupied the deeper parts of the tympanic recess and the internal parts of the ear. Wandering females of the second generation were found on the head and neck of this moth, but the left ear was unoccupied and undamaged. The moth was still alive when the photograph was taken, but died soon after—not necessarily from the effects of its parasites. Another moth of the same species survived a similar infestation for 16 days.

hours are required, with the moth unrestrained, for the mites to reach and perforate the tympanic and countertympanic membranes and to begin egg laying. It is during this time, of course,

that the "choice"[1] of ears is made. What goes on during this critical interval?

The possibilities appear to be limited: (a) the two ears are not equivalent, and each mite might find its way unaided to the more attractive or accessible one; (b) the mites might follow a leader whose choice could be random; (c) each might follow an innate behavior pattern dictating that it should seek the second ear unless it finds another mite in the first.[2] The actual solution of the problem, though differing from any of these conjectures, seems to partake somewhat of all three. The first mite may make a random choice, but does not normally visit both ears. Succeeding mites follow the same path as the first, but only from a critical point at which each arrives independently by an apparently innate routine.

The observations which led to this conclusion were delayed for several seasons by the mistaken assumption that one could not follow the movements of the mites on a free and unrestrained moth. Once it was realized that this is not true, it was but a short time before the assembly of the wanderers to form unilateral colonies had been observed repeatedly. Many moths after a few hours of evening activity settle down to a long rest which may last for the rest of the night and all the next day. At such times the moths are not too easily aroused and may be kept under the microscope without restraint for long periods. They are evidently not disturbed by the activities of the mites. For critical observations decapitated moths may be used. These stay indefinitely in a normal resting position, moving briefly only when touched. On resting normal or headless moths the mites, though often completely hidden in the vestiture, reveal their position at every movement by the displacement of the hairs, and can thus be followed quite readily.

Until shortly before they reach the ear, the mites seem to be guided by the moth's contours and by the distribution and orientation of its hairs and scales. Figure 2 is a dorsal view of *Pseudaletia* (= *Leucania* = *Cirphis* = *Heliophila*) *unipuncta* (Haworth), the armyworm moth, in the resting position, show-

[1] Lest the word "choice" be considered objectionable, it may be stated that no deliberative action is implied here or elsewhere in this paper.

[2] This amusing and ingenious suggestion was made by Dr. Horst Mittelstaedt.

ing the chief areas traversed by the mites and mentioned in the following account. The thoracic vestiture in this species is close and smooth. It consists of a mixture of simple, elongate,

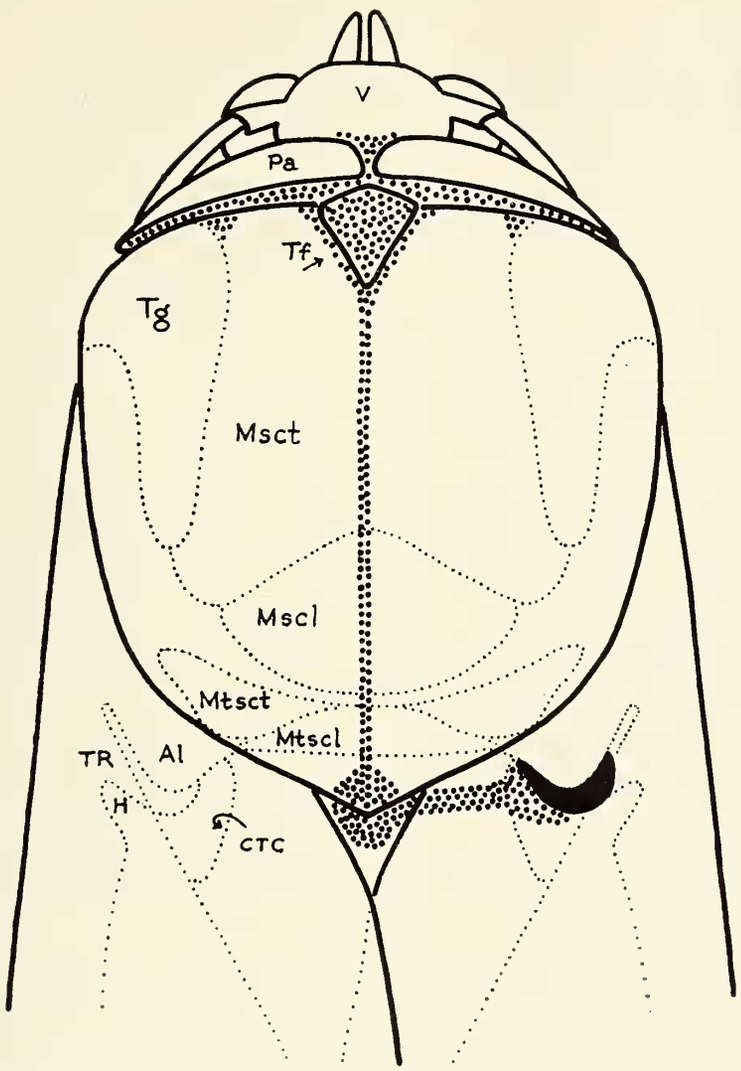

Figure 2. *Pseudaletia unipuncta,* semi-schematic dorsal view of anterior portions. Heavy lines indicate outlines of superficial features; light dotted lines, outlines of skeletal elements. Heavily dotted areas show the chief pathways traversed by the mites in reaching a colony site (shown in black) in the right tympanic recess. Al, alula of hind wing; CTC, orifice (shown by arrow) of countertympanic cavity; H, hood; Mscl, mesoscutellum; Msct, mesoscutum; Mtscl, metascutellum; Mtsct, metascutum; Pa, patagium; Tf, anterior mesothoracic tuft; Tg, tegula; TR, tympanic recess; V, vertex. The term "collar," as used in the text refers to the vestiture of the patagia; the term "disc" refers to the metascutum and metascutellum, collectively. Pathways of mites from the site of boarding to the collar region are not shown.

and spatulate scales overlain by simple, flattened, and spatulate hairs (cf. Forbes, 1954, p. 7–9). The distribution of these scale and hair types varies over different parts of the thoracic surface

Near the center of the disc, long, simple hairs predominate in the upper layers, and the convergence of the free tips of these hairs from the two sides marks the midline (an important part of the mites' path) from the anterior mesothoracic tuft to and slightly beyond the rear margin of the thorax. There the converging hairs form a little, pointed brush, meeting the first abdominal tuft between the inner margins of the folded forewings. The anterior thoracic tuft is a spray of long simple hairs on the anteromedial part of the mesonotal disc. Rimming and somewhat overlapping the disc anteriorly is the "collar" of mixed hair and scales that curve upward and rearward from the anterior surfaces and upper borders of the patagia.

Just behind the metascutellum, the surface of the first abdominal tergum dips downward slightly to form a shallow transverse trough or groove extending between the dorsal lips of the countertympanic cavities of either side. In a resting moth, this trough is roofed laterally by the forewings and medially by the projecting brush of thoracic hairs. It is bordered anteriorly by the metascutellum and posteriorly by the hair tufts of the first abdominal tergum. On its floor is a carpet of very small, closely appressed, simple scales, free from the admixture of hair. The transverse trough forms a natural external pathway between the two ears, quite concealed from view until the wings and overlying vestiture are removed.

When a fertile female mite is placed upon or allowed to board a resting moth she promptly buries herself among the hairs wherever she happens to be. She moves slowly among their bases in a hesitant, groping manner, punctuated by peculiar little jerks or darts which do not send her forward appreciably but which may serve to test the orientation of the hairs or to adjust her position among them. Her course, though irregular, is toward the collar or the neck, which she eventually reaches. The route depends partly, of course, upon the site of boarding, and does not appear to be fixed in any systematic way. Once arrived, the mite remains in the neck or collar area for some time. She may be quiet for long periods, occasionally rummaging about among the deep hairs or shuttling from one side to the other. There may be intermittent feeding through the soft membranes of these areas, and fecal droplets may be deposited among the hairs. One mite (on

a decapitate moth with loose collar vestiture) was seen to cross twice from a resting position at the left shoulder to right postpatagial region, each time leaving a fecal droplet in the same spot and returning immediately for another period of rest or feeding.

The time spent in the collar region seems to depend upon the alimentary or reproductive state of the mite rather than on the condition of the moth, the time of day, or other extrinsic factors. Some mites, perhaps unready for oviposition, remain there indefinitely after experimental transfer. Gravid females usually stay no longer than an hour or two. During this period there is no indication that the mite is seeking any other location. To all appearances she has made herself at home and is going to stay there.

The second phase of activity, which ends in the mite's arrival in the ear, is heralded by a rather sudden increase in the tempo of the movements in the collar region. Now the mite seems in a hurry, and her actions give the impression of impatient seeking for something. She approaches the anterior tuft and probes this way and that among the hairs at its base or sides. Soon the long hairs are parted like tall grass at a point near the midline. From the center of the "part" the mite emerges. She continues to push aside the hairs with her forelegs, making a broad path down the center of the disc. She creeps quickly along this path, extending it rearward as she goes, and pausing briefly now and then to lift or probe the scales that form its floor. There are no longer the jerky or darting movements that characterized her earlier actions, and there is no hesitation or turning aside until the brush at the posterior border of the thorax has been reached. This is the base of the triangle bordered by the forewings at the center of the transverse trough (Figure 2).

If the mite is already engorged she has some trouble in getting down among the tufted hairs of this region and into the trough itself, but she persists, and at last, within one or two minutes of the time her rearward march was started, she reaches the crossroad, midway between the two ears, where her final direction must be determined. Here she probes repeatedly in all directions, turning first one way and then another, making many tentative starts and returning to the midline after a step or two. Even-

tually the die is cast: she goes to one side and under the wing margin, raising it slightly as she disappears. She is now wholly concealed from observation or detection, but if the host is quickly anesthetized she is found in or just outside the tympanic recess of the side on which she was last seen.

This, it might be supposed, is the end of the journey; but it is not. Time after time, at intervals of about ten minutes for the next hour or more, she returns to the "crossroad," probes briefly in various directions as before, and then goes back to the ear first occupied. After seven or eight such visits, she finally settles down to the business of forming a colony. The third and last phase of her wandering is ended. But why the retracing of steps? Is it merely that she is still "undecided," or is this a functional part of her routine?

The problem of unilaterality in compound colonies is not solved, of course, by knowing the behavior of the first mite to arrive. It is the actions of the others that must tell the story. If a second mite is placed upon the moth, either at the same time as the first or later, it goes through the same general behavior pattern as the first, and in the initial phase quite independently of her predecessor's path. If the two mites meet in the collar region, their contact is brief; there is no obvious sign of recognition, no tendency to congregate or for either mite to follow the other's trail. The midline march of the second mite may begin at a different point from that of the first (for example, on the opposite side of the thoracic tuft) but is completed in the same way as if the moth had been previously unoccupied. It is only at the "crossroad" that the behavior of the second mite appears significantly different from that of the first. The newcomer shows less hesitation. After only brief probing, she goes to the occupied ear, from which she, in turn, may revisit the crossroad area, though as a rule not so often as the first arrival. A third mite, or a fourth, or a fifth will follow the same procedure but with less hesitation at the crossroad, each turning toward the occupied ear from this point as though following a well-marked trail. If one of these mites is later removed from the ear and transferred to the head of the same moth or of another, it proceeds as before except that the time in collar region may be somewhat shortened. A brood female removed from her eggs and transferred to the

head or thorax of a mite-free moth will not necessarily go to the same side as that of its former home, but may settle on the side opposite, showing that a given mite is not, either congenitally or by habituation, "right-" or "left-handed."

On resting moths with folded wings, the mites have never been seen to visit the unoccupied ear. If the forewings are removed, however, such visits sometimes occur, though no bilateral colonies have resulted from them. Moreover, when the moth's forewings are removed the first approach to the ear may be somewhat different from that described above. Only two such cases have been studied. In both, the mites wandered considerably on reaching the crossroad area and did not appear to find or recognize the transverse path immediately. One went as far rearward as the second segment of the abdomen, then turned obliquely forward and moved against the direction of the hair in this region until she reached the tympanic area. In one such moth the mites, having reached the ear, proceeded to distribute fecal droplets along the sides of the transverse path, and in this way made a mat of hairs which gradually converted the exposed passage into a thinly roofed tunel extending clear across the dorsum. Such hair mats normally cover the external tympanic recess in mature colonies, but are not normally found on the dorsum. It was thought at one time that the slight symmetry of the overlapping forewings might guide all the mites to the same ear. Since in a given moth the wings do not always overlap in the same way, if at all, and since bilateral colonies have not been formed when the wings were removed, this idea was soon given up.

From the facts at hand, one may infer that until it is nearly ready to start egg laying and has reached the "crossroad" between the two ears, each mite obeys an innate behavior pattern for which the topography of the vestiture supplies the effective stimuli. At the crosroad, the choice of ears by the first mite could be at random, but succeeding mites are apparently influenced at this point by the previous behavior of the first. The nature of this influence remains unknown, but very likely it is concerned with the frequent retreading of the path between the chosen ear and the midline. It could be in the nature of a chemical trail, secreted, perhaps as a prelude to egg laying, after the colony site has finally been adopted. It is certainly not a simple

result of the perforation of the tympanic membrane by the first mite to arrive, for the experimental puncture of the membrane does not attract mites to the damaged ear. Many more observations are needed to clear up this and other puzzling points.

If the second mite does not arrive in the ear until after the first has produced an egg clutch, she may be greeted by a display of "hostility" that is offset only by persistent attempts to gain access to the tympanic air sac. This behavior has been described elsewhere (Treat, in press). It is remarkable that in the face of such a reception, the intruder does not seek the unoccupied ear. The fact that it does not do so testifies to the potency of the influences promoting unilaterality, and, no doubt, to the high selective value of that condition.

SUMMARY

When several fertile females of the moth ear mite board the same prospective host, they go at first to the collar region, from which, some time later, they proceed singly along the dorsal midline to a point midway between the two ears. Thence their course appears to be determined by the actions of the first mite to arrive, with the result that all the mites assemble in one ear to form a compound, unilateral colony.

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